Agonistic behaviour among *Haemulon* spp. (Actinopterygii: Haemulidae) and other coral reef fishes in Northeastern Brazil

by

Pedro Henrique CIPRESSO PEREIRA* & Beatrice PADOVANI FERREIRA (1)

ABSTRACT. - Food resource competition and habitat segregation motivate agonistic interactions among coral reef fishes. The present study analyses the relationships of agonistic encounters according to trophic guilds and life phases of fishes of the genus *Haemulon* in Northeastern Brazil. The individuals of this genus display the highest aggressiveness towards invertebrate feeders (90.1% of total percentage) and carnivores (6.4%), the two trophic guilds with which food preferences overlap. Meanwhile, they were attacked more by territorial herbivores from the genus *Stegastes,* 76.2% of total percentage (e.g. *S. fuscus* and *S. variabilis*). Adults performed more agonistic interactions than juveniles ($Z = 2.45$; $p < 0.05$), probably in relation with their larger body size and more solitary habits.

RÉSUMÉ. - Comportement agonistique des *Haemulon* spp. (Actinopterygii : Haemulidae) et autres poissons des récifs coralliens au nord-est du Brésil.

La compétition pour les ressources alimentaires et la ségrégation des habitats suscitent des comportements agonistiques chez les poissons de récifs coralliens. Cette étude analyse les relations d'agressivité entre espèces en fonction des guildes trophiques ainsi que des phases de vie des espèces du genre *Haemulon,* au nord-est du Brésil. Les individus de ce genre se montrent plus agressifs envers les consommateurs d'invertébrés (90,1% du pourcentage total) et les carnivores (6.4%) car leurs préférences alimentaires se recouvrent avec celles des deux guildes trophiques. De plus, ils sont plus attaqués par des herbivores territoriaux du genre *Stegastes,* 76.2% du pourcentage total (e.g. *S. fuscus* et *S. variabilis*). Les adultes montrent plus de comportements agonistiques que les juvéniles ($Z = 2,45$; $p < 0,05$), probablement en raison de leur grande taille et de leur mode de vie plus solitaire.

Key words. - Haemulidae - *Haemulon* spp. - Western Atlantic - Food resource competition – Aggressiveness - Agonistic encounters - Grunts.

The wide variety of trophic guilds, high species diversity, and individual abundances on coral reefs results in large numbers of agonistic behaviours among reef fishes. Agonistic behaviours can be observed between territorial, non-territorial, or both types of species (Robertson *et al.,* 1976). These interactions are mainly due to competition for food resources, although they may also occur as a result of competition for space and/or habitat segregation (Grant, 1997; Johnson *et al.,* 2011).

Territorial species normally display agonistic interactions toward fishes and invertebrates, and significant attention has been given to damselfishes of the genus *Stegastes* (e.g. Draud and Itzkowitz, 1995; Menegatti *et al.,* 2003; Osório *et al.,* 2006; Medeiros *et al.,* 2010; Souza *et al.,* 2011). Territorial behaviour is usually performed by fishes in order to reduce the number of external competing individuals. The level of aggressiveness displayed by territorial fish species vary from low in species with weaker association with particular reef zones, like surgeonfishes (Acanthuridae) to high among species showing strong territorialism, such as members of the Pomacentridae family (Robertson and Polunin, 1981; Letourneur, 2000; Alwany *et al.*, 2005).

Individuals of the genus *Haemulon* are known to display some degree of territorialism often displaying agonistic behaviour towards *Haemulon* spp. and other coral reef fish species (Motchek and Silva Lee, 1975; McFarland and Hillis, 1982; Burke, 1995; Verweij *et al.,* 2006). Agonistic interactions among individuals of this genus can be related to anti-predation mechanisms, lower energy expenditures, or competition for food resources (McFarland and Hillis, 1982). Grunts' aggressiveness increases with size and occurs more often during early morning and late afternoon (McFarland and Hillis, 1982).

The genus *Haemulon* (family Haemulidae) contains 21 nominal species distributed throughout the world (Rocha *et al.,* 2008). Fifteen species of *Haemulon* are found in the western Atlantic, and five in the eastern Pacific (with one nominally shared by both regions) (Lindeman, 1986; Rocha and Rosa, 1999). This genus numerically dominates tropical shallow-reef communities (with schools reaching into the

(1) Departamento de Oceanografia, CTG, Universidade Federal de Pernambuco (UFPE). Av. Arquitetura, s/n, Cidade Universitária, Recife, PE, 50670-901, Brazil. [beatricepadovani@yahoo.com.br]

* Corresponding author [pedrohcp2@yahoo.com.br]

thousands of individuals), and it constitutes one of the most important reef fish group in Brazilian reefs due to its abundance, commercial value, and trophic importance as both predators and prey (Lindeman and Toxey, 2002; Ferreira *et al*., 2004; Rocha *et al*., 2008; Pereira *et al*., 2011).

The present study analyzed the agonistic interactions among four species of the genus *Haemulon* (*H. aurolineatum*, *H. parra*, *H. plumieri* and *H. squamipinna*) as well as with other coral reef fishes, and discusses their relationships with species, trophic guilds and life phases.

MATERIALS AND METHODS

Study area

The present study was conducted in the reefs of Tamandaré, Pernambuco State, in Northeastern Brazil. Lines of coral reef formations in this reef complex are arranged parallel to the coastline and resemble fringing reefs (Maida and Ferreira, 1997). These reefs are within the limits of the Costa dos Corais Marine Protection Area (MPA) that extends for 135 km. The Costa dos Corais - MPA was the first federal conservation area created in Brazil that included coastal reefs. It is the largest MPA in the country and encompasses an area of approximately 413,563 hectares in two states (Maida and Ferreira, 1997; Ferreira *et al*., 2001).

Habitats surveyed comprised a relevant diversity of substrata, mostly in the first and second line of shallow reef habitats (Maida and Ferreira, 1997), and included algal beds, sandbanks, coral reefs and muddy bottom, with depth ranging from 0.5 to 6 m, and a maximum distance of 1.5 km from the land. Macroalgae from genera *Sargassum, Padina, Caulerpa, Udotea, Gracilaria, Dictyota,* and *Dictyopteris* compose the dense mats. The dominant coral reef species are *Favia gravida, Millepora* spp., *Montastrea cavernosa, Mussismilia* spp. and *Porites astreoides* (Maida and Ferreira 1997).

Behavioural observations

Behavioural observations were performed during a one year period (from December 2009 to December 2010) using snorkeling and SCUBA diving techniques. Observation was carried from early morning (8:00) until late afternoon (17:00), when the focal-animal sampling technique was employed (Altmann, 1974; Lehner, 1979).

Each observation session was standardized at 10 min-

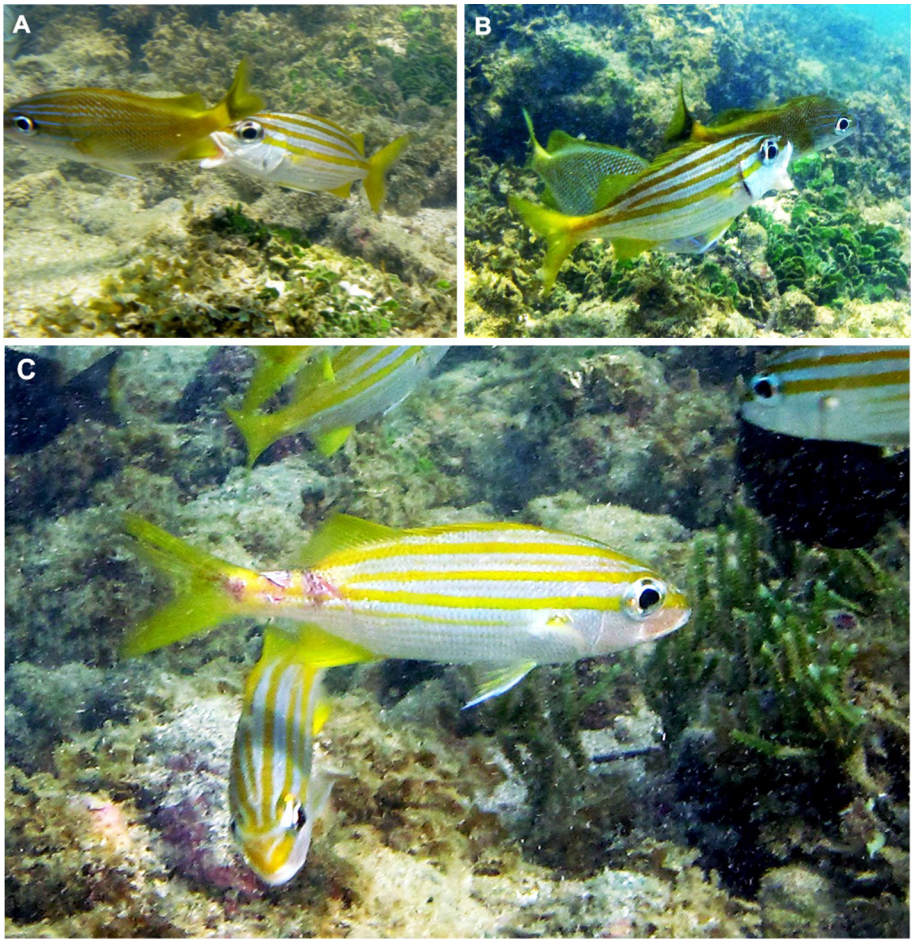

Figure 1. – **A**: Active agonistic interactions undertaken by *Haemulon squamipinna* and *H. plumieri*. **B**: Active agonistic interactions undertaken by *H. squamipinna* and two individuals of *H. plumier*.; **C**: Injury caused by a bite of an adult of *Stegastes fuscus* involved in one agonistic interaction with an individual of *H. squamipinna*.

Species	Haur (A ; J)	Hpar (A ; J)	Hplu (A ; J)	Hsqu (A ; J)	TOTAL
Haemulon aurolineatum adult	23 ; -	1 ; 0	-	5 ; 0	29
Haemulon parra adult	-	7 ; 0	2 ; 0	15 ; 0	24
Haemulon parra juvenile	-	2 ; 17	0 ; 3	-	22
Haemulon plumieri adult	-	2 ; 0	7 ; 0	-	9
Haemulon plumieri juvenile	-	0 ; 1	0 ; 9	-	10
Haemulon squamipinna adult	-	-	-	8 ; 0	8
Mulloidichthys martinicus adult	7 ; -	-	-	-	7
Pseudupeneus maculatus adult	5 ; -	4 ; 0	1 ; 0	-	10
Other species*	1 ; -	4 ; 5	8 ; 1	0 ; 2	22
Total	36 ; 0	20 ; 24	18 ; 13	28 ; 2	141

Table I. - Active agonistic interactions involving the genus *Haemulon* and other coral reef fish species. Data clustered by species and life phases (A: adult, J: juvenile). Haur = *H. aurolineatum*; Hpar = *H. parra*; Hplu = *H. plumieri* and Hsqu = *H. squamipinna*. * Interactions involving other species (n): *Acanthurus bahianus* adult (1), *Alfester afer* juvenile (1), *Epinephelus adscensiones* juvenile (1), *Haemulon plumieri* juvenile (3), *Halichoeres poeyi* juvenile (1), *Holocentrus adscensiones* adult (1), *Labrisomus nuchipinnis* adult (1), *Lutjanus alexandrei* juvenile (2), *Malacoctenus delalandii* adult (1), *Mulloidichthys martinicus* adult (1), *Ophioblennius trinitatis* adult (1) and *Sparisoma axillare* juvenile (1).

utes. Individuals were observed during this period and the number of agonistic interactions was established with other reef fishes recorded on PVC boards. Each species was classified according to a trophic guild. We considered four trophic guilds (territorial herbivores, roving herbivores, invertebrate feeders, and carnivores) according to Ferreira *et al*. (2004) and two life stages (juvenile and adult) according to Humann and Deloach (2002) and Lindeman and Toxey (2002). Forty observation sessions were conducted for each of the four species (20 adults and 20 juveniles), for a total of 160 ten-minute observation sessions, totalling 1600 minutes (26.6 hours).

The agonistic interactions observed were classified as:

a) Active agonistic interactions ("*to chase*"): undertaken by individuals of the genus *Haemulon* under observation, i.e. those animals showing aggression towards another species;

b) Passive agonistic interactions ("*to be chased*"): aggression initiated by another species of reef fish, directed towards a species of the genus *Haemulon*.

To compare the numbers of active and passive agonistic interactions between the different life stages (juvenile and adult) and also between different species of the genus, a non-parametric Mann Whitney U-test was applied, considering a 0.05% significance level (Zar, 1999).

RESULTS

A total of 141 active agonistic interactions performed by species of the genus *Haemulon* were observed. Those involved 16 species of reef fishes belonging to 10 families (Tab. I, Fig. 1). The species with the largest numbers of interactions were: *H. aurolineatum* adults (n = 29), *H. parra* adults (n = 24), *H. parra* juveniles (n = 22), *H. plumieri* juveniles (n = 10), *Pseudupeneus maculatus* adults (n = 10) and *Mulloidichthys martinicus* adults (n = 7). The most represented families were Haemulidae (106) and Mullidae (19).

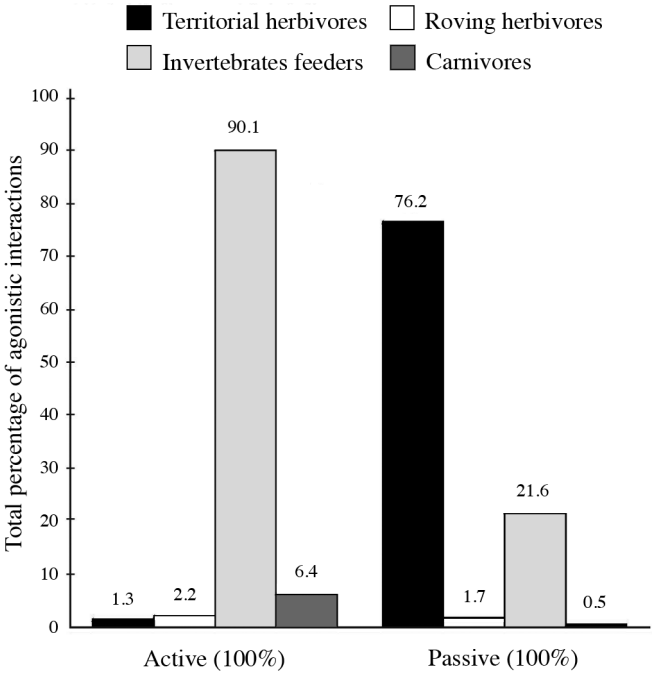

Figure 2. - Total percentage (%) of agonistic interactions (passive and active) of *Haemulon* spp. with data clustered according to trophic guild.

A total of 265 passive agonistic interactions involving individuals of the genus *Haemulon* were observed. They involved 18 reef fish species belonging to 11 families (Tab. II, Fig. 2). The species with the largest number of interactions were: *Stegastes fuscus* adults (n = 121), *S. fuscus* juveniles (n = 17), *S. variabilis* adults (n = 12) and *S. variabilis* juveniles (n = 53). The most represented families were Pomacentridae (203) and Haemulidae (45).

The species involved in agonistic interactions were grouped into trophic guilds (Fig. 2). Passive agonistic interactions performed by territorial herbivores (e.g. *S. fuscus* and *S. variabilis*) composed the majority (76.2%) of the record-

Table II - Passive agonistic interactions involving the genus *Haemulon* and other coral reef fish species. Data clustered by species and life phases (A: adult, J: juvenile). Haur = *H. aurolineatum*; Hpar = *H. parra*; Hplu = *H. plumieri* and Hsqu = *H. squamipinna*.

Species	Haur (A ; J)	Hpar (A ; J)	Hplu (A ; J)	Hsqu (A ; J)	TOTAL
Haemulon aurolineatum adult	-	3 ; 0	-	2 ; 0	5
Haemulon aurolineatum juvenile	-	0 ; 1	-	0 ; 6	7
Haemulon parra adult	-	-	0 ; 4	2 ; 0	6
Haemulon parra juvenile	-	0 ; 4	0 ; 3	-	7
Haemulon plumieri adult	-	-	0 ; 6	2 ; 0	8
Haemulon squamipinna adult	-	-	-	6 ; 0	6
Haemulon squamipinna juvenile	0 ; 3	-	-	0 ; 1	4
Lutjanus alexandrei adult	-	-	1 ; 3	-	4
Stegastes fuscus adult	16 ; 6	57 ; 16	8 ; 0	16 ; 2	121
Stegastes fuscus juvenile	-	0 ; 3	0 ; 14	-	17
Stegastes variabilis adult	1 ;	0 ; 3	0 ; 8	-	12
Stegastes variabilis juvenile	0 ; 1	3 ; 19	0 ; 26	0 ; 4	53
Other species*	-	2 ; 3	0 ; 5	4 ; 1	15
Total	17 ; 10	65 ; 49	9 ; 69	32 ; 14	265

ed encounters. However, active agonistic encounters were very frequent (90.1%) towards invertebrate feeders (e.g. *P. maculatus* and *Haemulon* spp.). The remaining interactions occurred with roving herbivores (e.g. *Acanthurus* spp. and *Sparisoma* spp.) and carnivores (e.g. genera *Epinephelus* and *Lutjanus*).

Analyses were performed involving the numbers of agonistic interactions at the different life stages (adult *versus* juvenile) of species of the genus *Haemulon*. Significant differences were identified regarding active interactions ($Z = 2.45$; $p < 0.05$), with adults performing more active agonistic behaviours (72.3%) than juveniles (27.6%). On the other hand, juveniles were subjected to 53.5% of passive interactions than adults, but the difference was not statistically significant ($Z = 5.43$; $p > 0.05$).

There was no clear pattern regarding the numbers of passive and active agonistic interactions considering each species separately (Fig. 3), and no significant differences were seen between them ($Z = 1.89$; $p > 0.05$) (Fig. 3). *H. parra* was involved in more agonistic interactions (passive = 28.3%; active = 43.0%), *H. aurolineatum* had the lowest number of passive interactions, while *H. squamipinna* had the lowest number of active interactions.

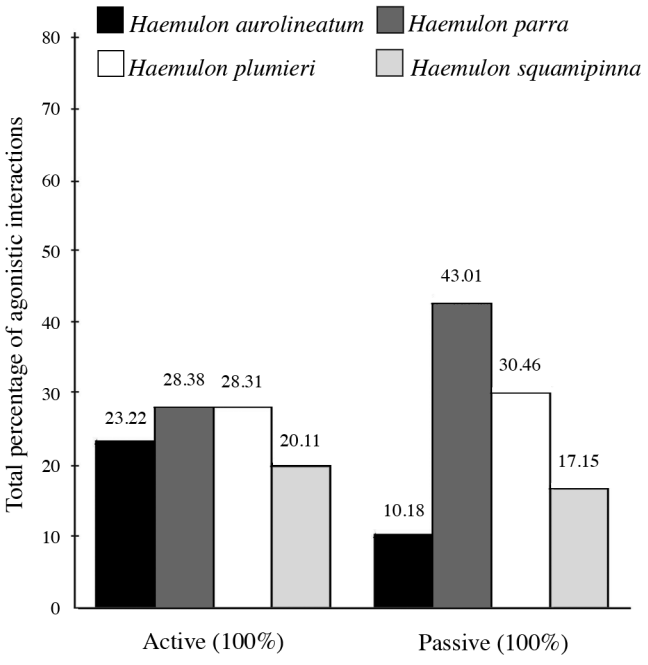

Figure 3. - Total percentage of agonistic interactions (passive and active) of *Haemulon* spp. with data clustered by species.

DISCUSSION

The occurrence of agonistic interactions among reef fishes is usually related to competition for limited resources such as food and habitat (Grossman, 1980; Johnson *et al*., 2011). Aggressiveness is not related only to competition, however, since other characteristics of the species biology and its ontogenetic shifts can also influence their relationships with the reef community (Jones, 1987).

Although for some fish species a greater frequency of agonistic interactions involving juveniles is observed compared to adult phase individuals (Leum and Choat, 1980), it is usually reported that the frequency of agonistic interactions tend to increase as individuals grow. This pattern has been observed for several reef fish families: Pomacentridae (Menegatti *et al*., 2003; Souza *et al*., 2011), Labridae (Jones, 1984), Lutjanidae (Mueller *et al*., 1994), and Haemulidae

(McFarland and Hillis, 1982) as recorded in the present study, where 72.3% of agonistic actions were carried out by adults. This fact is probably related to the larger body size of the adult individuals of the genus *Haemulon*, their accession in the dominance hierarchy, and to the more solitary habits of adults (McFarland and Hillis, 1982). For territorial species, increase in agonistic behaviour is also related to growth, and directly associated to the expansion of the territories defended by adults (Medeiros *et al*., 2010).

When displaying agonistic behaviour, individuals of the genus *Haemulon* assume a series of characteristic aggressive postures, including: "mouth-to-mouth pushing", "jaw biting", "lateral display" and "erection of the dorsal fin", as observed by McFarland and Hillis (1982) for *H. flavolineatum* and *H. plumieri* in the Caribbean region. Displays of all of these positions were observed for the *Haemulo*n spp. analyzed in this study, confirming the uniformity of agonistic behaviour patterns in this family. The same pattern of agonistic behavior was observed for other coral reef fishes species belonging to the Pomacentridae (Osório *et al*., 2006; Medeiros *et al*., 2010; Souza *et al*., 2011) and Acanthuridae (Alwany *et al*., 2005) as well as for freshwater cichlid fishes (Yamamoto *et al*., 1999).

The active agonistic interactions demonstrated by individuals of the genus *Haemulon* occurred almost entirely when confronting invertebrate feeders (e.g. families Mullidae and Gerreidae) or other individuals of *Haemulon* spp. The trophic guild formed by mobile invertebrate feeders (MIFs) has the highest relative abundance on coastal reefs at Tamandaré (Ferreira *et al*., 2004). The fact that these species shows greater aggressiveness with species that have similar feeding habits confirms the hypothesis that agonistic interactions among reef fishes are related to competition for food resources and that they increase with greater food resource overlap (Orians and Wilson, 1964; Draud and Itzkowitz 1995), as food is considered to be the main competed resource among fish (Zaret and Rand, 1971; Mittelbach, 1984).

Species from the genus *Stegastes* performed the largest number of agonistic interactions towards individuals of the genus *Haemulon* (76.2% of the total). As *S. fuscus* performed twice the number of agonistic encounters as *S. variabilis,* it would seem to confirm the observation that *S. fuscus* is more aggressive than *S. variabilis* (Medeiros *et al*., 2010). However, this result may simply be related to the greater abundance and size of *S. fuscus,* that was twice as much abundant than *S. variabilis* in the reef environments studied here (Schwamborn and Ferreira, 2002) and reaches larger body sizes (Pacheco, 2008).

The agonistic encounters of these species were related to two different situations: 1) the adults of the genus *Stegastes* excluded individuals of the genus *Haemulon* only in competition for territory and for habitat segregation (i.e., asymmetric competition) since grunts do not use algae territories as food resources, 2) aggressions by juvenile *Stegastes* spp. could be a possible competition for food resources with juvenile *Haemulon* spp. Several studies (Lobel, 1980; Letourneur *et al*., 1997) have reported high frequencies of occurrence of invertebrates in the stomach contents of juvenile *Stegastes* spp. individuals, demonstrating that they can feed on invertebrates associated with algae, as juveniles of *H. parra* and *H. plumieri* (Pereira and Ferreira, unpubl. data). Corroborating the idea of competition for food resources, Medeiros *et al*. (2010) also observed large numbers of agonistic encounters among *S. variabilis* and invertebrate feeders, especially *Haemulon parra,* in the Northeastern Brazil.

Reef fishes from the family Pomacentridae (e.g. *Stegastes* and *Pomacentrus*) notably territorialist species, perform agonistic behaviors as a major adaptive advantage (McDougall and Kramer, 2006) ensuring food resources and nest sites within their territories (Johnson *et al*., 2011). For the *Haemulon* spp. the aggressive behavior observed in this study may be associated with high levels of hormone as noted by Sloman and Armstrong (2002) for other fish species (e.g. natural aggressiveness). Moreover, it also can be related to an adaptive advantage to the relatively small body size and up to the successful colonization of different habitats, since it is known that grunts are abundant in both natural and artificial reefs (Brotto *et al*., 2007; Rocha *et al*., 2008), seagrass beds, estuaries and mangroves (Verweij *et al*., 2006).

Thereby, a large number of agonistic interactions between species of the genus *Haemulon* were observed in the present study and can be directly associated with some degree of territorial behavior performed by grunts (McFarland and Hillis, 1982; Burke, 1995). These species share similar foraging behaviour patterns (feeding rates and substratum choices) and diets (Pereira and Ferreira, unpubl. data), motivating considerable competition between individuals. Additionally, the species of this genus performed mixed schools, protective mimicry and foraging facilitation behaviour with them as well as with other coral reef fishes (McFarland and Hillis 1982; Pereira *et al*., 2011; Pereira *et al*., in press), therefore maintaining strong links between the species and the complex hierarchical relationships that greatly contribute to the occurrence of agonistic behaviours.

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